

A review of symbiosis in the Bivalvia, with special attention to macrosymbiosis

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Abstract. The symbiosis (defined as a strict interspecific association) between bivalves and other organisms is examined. Microsymbiosis (i.e., symbiosis with microorganisms) is frequent among Recent bivalves, and has been proposed to explain the unusual characters of several fossil bivalves. However, a critical review of the morphological criteria used to infer microsymbiosis in fossil bivalves shows that their application is likely to result in a large number of false positive and false negative results. Symbiosis with macroscopic organisms (i.e., macrosymbiosis), on the other hand, has a better chance of being recognised correctly in fossils, although direct preservation of the associated organisms remains the only completely safe criterion. Recent and fossil instances of macrosymbiosis are reviewed, and new evidence is presented to clarify the adaptive significance of some of these associations.

Key words: Bivalvia, chemosymbiosis, commensalisms, functional morphology, Lingulidae, Mollusca, parasitism, photosymbiosis, Porifera, Scleractinia, symbiosis

Introduction

Symbiosis was originally defined as a strict, usually obligatory association of individuals belonging to two or more species (Bary, 1879). This definition does not imply that the association is mutually advantageous to the organisms involved. Only subsequently was the term used with the latter meaning. The present paper follows the original definition of symbiosis, since no other concise term is available to characterise an interspecific association without connotations of usefulness to the involved organisms. Use of the terms commensalism and parasitism, for instance, requires that the life habits and the advantages and/or disadvantages to the species involved are known.

For the purposes of this paper, two categories of symbiosis can be recognised among bivalves. The first involves microscopic endosymbionts living in a bivalve host. This category can be characterised as microsymbiosis. The second category involves macroscopic organisms associated with bivalves, and can be called macrosymbiosis. This paper concentrates on the latter category, but a discussion of microsymbiosis is useful as an introduction, because this subject has received considerable attention by palaeobiologists (see references below). In addition, this theme illustrates several of the problems that characterise the recognition of macrosymbiosis in the fossil record.

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author.

Microsymbiosis

Photosymbiosis

Most of the literature on symbiosis in bivalves deals with microscopic endosymbionts hosted by bivalves. In particular, photosymbiotic zooxanthellae and the associated adaptations of the hosts have been studied in the Recent Tridacnidae (Yonge, 1936; Purchon, 1955; Stasek, 1961, and references therein) and Cardiidae (Kawaguti, 1950, 1968, 1983; Hartman and Pratt, 1976; Jacobs and Jones, 1989; Jones and Jacobs, 1992). The host bivalves show a range of cytological adaptations to the symbionts, as well as microstructural and macroscopic adaptations in shell morphology (e.g., see above references, and Seilacher, 1972, 1973, 1990).

Among these bivalves, the Tridacnidae build extremely large and thick shells thanks to photosymbiosis, and their ventral commissure (uppermost in the life position) is modified to maximise exposure of the mantle tissues to sunlight. In some species, sculpture on the external shell surface further increases the mantle area exposed to light (above references).

The cardiid *Corculum* has an antero-posteriorly flattened, semitransparent shell to optimise the exposure of the mantle to sunlight passing through the shell. The posterior shell slope possesses numerous semitransparent windows, which

result from a peculiar type of shell pigmentation rather than from a specialised microstructure (Watson and Signor, 1986).

Other Recent bivalves are known to possess photosynthetic endosymbionts. Among them are the freshwater unionid *Anodonta* (Goetsch and Scheuring, 1926) and the trapeziid *Fluviolanatus subtorta* (Morton, 1982). The significance of these associations has not been studied in detail. Other bivalves are frequently infected by microscopic algae (e.g., the Recent pectinid *Placopecten magellanicus*; Naidu and South, 1970; Naidu, 1971). Although these can be characterised as instances of parasitism by the alga, they are interesting in that they constitute a possible evolutionary stepping-stone toward a mutually advantageous situation.

The adaptive significance of photosymbiosis is not uniform among bivalves. In the Tridacnidae, photosymbionts are an important food-source for the host, and they allow the construction of very large and heavy shells (above references). In all other studied instances, however, the bivalves are relatively small, and their shells thin or only moderately thick. In at least part of these cases, the spectrum of sunlight appears to be selectively filtered by the mantle tissues of the host in order to fine-tune the metabolic products of the photosymbionts (above references).

A few palaeontologists (e.g., Kriz, 1979; Yancey, 1982; Yancey and Boyd, 1983; Seilacher, 1990) have proposed photosymbiosis in a broad range of fossil bivalves, using morphological convergence with *Tridacna* and/or *Corculum* to support their theses. These fossil bivalves range in age from the Palaeozoic to the Caenozoic, belong to several superfamilies, and possess extremely large and/or thick shells, or antero-posteriorly flattened and presumably translucent *Corculum*-like shells.

The reliability of these morphologic criteria to infer photosymbiosis in fossil bivalves, however, is questionable. With the exception of *Corculum* and the Tridacnidae, Recent photosymbiotic bivalves show little or no morphological specialisation of the shell to photosymbiosis. In addition, while photosymbiosis in *Tridacna* is directly related to increased shell secretion and affects its stable-isotope composition (above references), such phenomena are absent in other Recent photosymbiotic bivalves (Jones and Jacobs, 1992). Nonetheless, stable-isotope analysis can be used in fossils when one desires to test whether shell secretion was aided by photosymbiosis, in a manner convergent to the Tridacnidae. Such an analysis led Jones, Williams and Spero (1988) to exclude photosymbiosis (or at least its involvement in shell secretion) in the Pliocene *Mercenaria "tridacnoides"*. This bivalve is a morph of *M. campechianensis*, and differs from the latter in a shell with a wavy or zigzag ventral commissure. Seilacher (1990) had earlier proposed photosymbiosis in this form, based on shell morphology.

Finally, one may test the reliability of the above morphologic criteria by applying them to Recent bivalves. There are several living bivalves which have at least one of the morphologic characters mentioned above. Among these are large and thick-shelled Ostreidae, Spondylidae, Pectinidae and Arcidae. However, none of these bivalves are known to host photosymbionts.

A flattened and translucent shell in an epifaunal bivalve is

not a reliable indication of photosymbiosis, either. A very good example is the Recent anomiid (or placunid) *Placuna placenta*. This species possesses a laterally flattened, thin and very translucent shell (Yonge, 1977, regarded this species as the most flattened bivalve), and is a recliner on the surface of soft sediments in shallow water. Incidentally, the shell of this species was commonly used by the human population of the Philippines for the construction of house windows, before glass became broadly available. In a fossil species, such a shell might be regarded as an indication of photosymbiosis. However, *P. placenta* apparently hosts no photosymbionts. Although I am not aware of any explicit statement to this effect in the literature, the soft tissues were studied extensively by Yonge (1977), who most likely would not have failed to observe photosymbionts if they had been present.

Other Recent species of *Placuna*, like *P. ephippium*, are even larger than *P. placenta*. In *P. ephippium*, however, a reddish or brown pigmentation of the internal shell layer reduces shell translucency, and could be adaptive in sheltering the soft tissues from sunlight. Presumably, this pigmentation would be lost in fossilised material, leading an observer to conclude incorrectly that the shell was translucent like the one of *P. placenta*.

A further example is the Recent endolithic pectinid *Pedum*, which exposes a broad surface of ventral mantle tissues to the ambient light, in a fashion not unlike the Tridacnidae. The mantle tissues of *Pedum* are heavily pigmented and resemble the brightly-coloured ones of the Tridacnidae. However, this species hosts no photosymbionts (Savazzi, 1998). The broad expanse of exposed mantle tissues in *Pedum* does not appear to be adaptive by itself, and is rather a consequence of the mode of growth of this bivalve (see also below).

The presence of a prismatic or fibrous shell microstructure in some large fossil bivalves has been advocated in support of the photosymbiosis hypothesis, on the grounds that such a structure could conduct light well, working like a bundle of optical fibres (e.g., Seilacher, 1990). However, this type of light transmission has not been verified in Recent shell material. In particular, it is not known whether the sides of the prisms (which in living bivalves are interfaces between calcite and organic matrix) act as reflectors, or whether the refraction index at the periphery of the fibres is different from the one at its centre. Either condition is indispensable for the fibre to function as a light guide. The fibrous layers of some fossil bivalves do seem to act as optical fibres, but this could be misleading, since the organic shell matrix in this material was likely lost or altered during diagenesis, so that the prism sides are now calcite/air interfaces with optical properties different from the original ones. In addition, the optical properties of fibrous layers could be irrelevant, because sunlight may have been absorbed by additional shell layers with different microstructures (which, in addition, may have disappeared through selective diagenetic solution), or by a pigmented periostracum or organic shell matrix (see also above).

In conclusion, when performing this type of functional reconstruction, it should be remembered that morphologic criteria alone are unreliable, since flattened and/or thickened

shells may have several adaptive explanations. Therefore, many instances of photosymbiosis inferred from large and thick shells, translucent shells and/or flattened shell geometries in fossils are likely false positives, while most of the true instances of photosymbiosis in fossils are likely to pass undetected.

A few fossil bivalves with highly specialised morphologic features may have been photosymbiotic. This is the case, for instance, of some rudists (Vogel, 1975; Seilacher, 1998, and references therein). Shell morphology indicates that, in several representatives of this group, a well-developed system of mantle diverticula occupied cavities within the shell, and in some cases was also exposed to the outer environment. However, it must be stressed that, based on palaeoenvironmental reconstructions, as well as on the lack of the above morphological features in most rudists, photosymbiosis must have been restricted to few representatives (see Jablonski, 1996).

Another candidate for symbiosis is represented by the Triassic wallowaconchids (Yancey and Stanley, 1999), in which the wing-like lateral carinae of the large *Corculum*-shaped shells were subdivided into partitions by radially-growing septa and, presumably, occupied at least in part by finger-like extensions of mantle tissues. This morphology is compatible with photosymbiosis (assuming the shell was translucent) as well as chemosymbiosis (assuming that the shell cavities housed chemosymbionts). However, septation of the carinae may be functional as a lightweight mechanical reinforcement, and a critical analysis of the symbiosis hypothesis shows that no septa, or at most a single septum separating the space within the carina from the rest of the shell cavity, are required for both photosymbiosis and chemosymbiosis to take place.

In these and comparable instances, photosymbiosis should be regarded as a reasonable hypothesis only if (1) the observed morphology satisfies all requirements for photosymbiosis, and (2) alternative functions for the observed morphology can be discarded. In the rudists with exposed mantle tissues, for instance, one should try first to eliminate the possibility that the mantle functioned as a ciliated carpet for the collection of food particles. In the case of rudists with shell diverticula, one should exclude alternative functions like brood pouches, cavities for the "farming" of chemosymbionts, structures for discouraging attacks by shell borers, energy-absorbing "bumpers" that would stop impact cracks from propagating to the inner shell layers, and lightweight shell structures like those observed in Recent soft-bottom oysters (e.g., cf. Chinzei, 1995). If these precautions are taken, unusual morphological adaptations like those of the rudists and wallowaconchids may be more reliable in inferring instances of photosymbiosis than general criteria based on large massive shells or antero-posterior shell flattening.

Chemosymbiosis

Chemosymbiosis appears to be more common than photosymbiosis among Recent bivalves. In addition to deep-water forms, like *Calyptogena*, which are associated with hydrothermal vents (e.g., Hashimoto *et al.*, 1989; Horikoshi, 1989) or hydrocarbon seeps (Childress *et al.*,

1986), several deep-infaunal bivalves from shallower water rely on bacterial chemosymbionts. These forms rely on bacteria that oxidise sulphide or methane (above references). In several cases (e.g., the Lucinidae, *Solemya*), the chemicals necessary to feed the symbionts are drawn to the mantle cavity by pumping pore water from deeper, anoxic layers of sediments (Felbeck *et al.*, 1983; Dando *et al.*, 1985, 1986; Reid and Brand, 1986). At least in some of these bivalves, elemental sulphur can be stored within the organism, possibly as a means to store energy (Vetter, 1985).

Solemya and *Lucinidae*.—*Solemya* builds Y-shaped burrows, and collects water from underlying, oxygen-poor and nutrient-rich sediment through the lowermost branch of its burrow (Stanley, 1970, pl. 3; Seilacher, 1990). Lucinids use the highly extensible foot to build a system of narrow canals with a comparable function (e.g., see Stanley, 1970, pls. 15–18).

Fossil burrows of *Solemya* (or bivalves with similar habits) have been described as ichnotaxa (Seilacher, 1990), and the burrows of lucinids are potentially preservable. These ichnostructures can be used to detect indirectly chemosymbiosis in these and similar bivalves. However, one must keep in mind that several burrowing bivalves build a single siphonal gallery directed downwards (e.g., see Stanley, 1970). This gallery leads the exhalant current deep into the sediment, and therefore cannot be related to chemosymbiosis.

Teredinidae.—Most Teredinidae are wood-borers and host symbiotic cellulose-digesting microorganisms in an enlarged gut (Turner, 1966, and references therein). Thus, these bivalves utilise the substrate as a food source. Chemosymbiosis is not directly reflected in morphological adaptations of the skeletal parts. However, the boreholes of the Teredinidae are uniquely long (up to 2 m) and slender (typically 5–20 mm in diameter), and can "snake" around obstacles and other boreholes, thus allowing these bivalves to utilise the substrate with a higher efficiency than any other wood-borers.

The Caenozoic to Recent teredinid *Kuphus* reaches very large sizes (over 1 m in length, with a diameter of up to 60 mm) and builds a thick calcareous tube. However, this form is not a wood borer but a secondary infaunal soft-bottom dweller (Savazzi, 1982a, 1999b). It is not known whether it utilises the substrate as a food source, and therefore its body volume, which is substantially larger than that of any wood-boring teredinid, remains unexplained.

Fresh-water bivalves.—The unionid *Pleiodon adami* from the African Pleistocene possesses a tube-like structure projecting from the antero-dorsal shell margin and parallel to the elongated hinge line. Seilacher (1990) suggested that this tube functioned like a pipette, in order to funnel pore water from underlying sediment layers into the mantle cavity. This would have avoided direct contact of the soft parts with the anoxic sediment. However, Savazzi and Yao (1992) found that other Recent and Pleistocene fresh-water bivalves of similar overall shell morphology (albeit possessing smaller or no anterior projections) burrow with the commissure plane conspicuously inclined, rather than subvertical as inferred by Seilacher for *P. adami*. In the latter species, a subvertical

orientation would seem to be optimal for siphoning pore water from deep within sediment, while a substantially inclined orientation like the one observed in other fresh-water bivalves would place the antero-dorsal pipe in an unfavourable position. Thus, chemosymbiosis would have required *Pleiodon* to assume a shell orientation unusual for these bivalves. Specimens recorded in the life position could help to shed light on this species.

Conclusions

In spite of numerous attempts, the feasibility of detecting reliably photo- and chemosymbiosis in fossil bivalves appears questionable. All the criteria discussed above for inferring photosymbiosis in fossil bivalves are likely to produce a large number of false positive and/or false negative results. Probably, the fossilised burrows of a few chemosymbiotic bivalves are so far the only reliable evidence of such life habits. However, it cannot be excluded that careful analyses and new evidence may reveal probable instances of photo- and chemosymbiosis among fossil bivalves.

Macrosymbiosis

Macrosymbiosis in bivalves has received a lesser attention than microsymbiosis, and it is legitimate to ask whether it has a potential for being recognised in fossil material. Macrosymbiosis can be subdivided into two broad categories. The bivalve may be embedded in a larger organism or attached to its outer surface, or the reverse situation may occur.

Embedded macrosymbiotic bivalves

Lithophaginae.—Several Recent species of the mytilid *Lithophaga* occur constantly within living scleractinian corals (e.g., Kleemann, 1980). This type of association dates at least from the Palaeogene (Krumm and Jones, 1993). Although each of these *Lithophaga* species is recorded from several species of host coral, they are never found in dead corals (which are inhabited by other species of *Lithophaga*, exclusively living in this habitat). The siphonal opening of the borehole is exposed to the external environment, and there is no indication that the bivalve exploits the host as a source of food. Most likely, the living substrate provides better protection (living corals grow, while dead ones are subjected to erosion and/or fouling by encrusters) and possibly a lesser degree of competition by other borers (living corals may be less subjected to bioerosion than dead ones, and the endolithic fauna of living corals is, at any rate, less diverse than that of dead substrates).

Boring in living scleractinians requires the veliger to settle on the epithelium of the host and to pierce it to reach the skeleton. Alternatively, the veliger could be ingested by a coral polyp and subsequently pierce its coelenteron lining. In either case, this appears to require a behavioural and/or biochemical specialisation. It is not known whether *Lithophaga* boring in live coral constitutes a monophyletic or polyphyletic group. These species, at any rate, cannot be distinguished reliably from dead-substrate species on the basis of shell morphology. Several (possibly a majority) of

live-coral *Lithophaga* possess a secondary calcareous coating on the outer shell surface. In several cases, this coating forms into structures (aristae, or sets of denticles) that protect the posterior shell commissure against predators (e.g., Savazzi, 1999b, and references therein). Most species of *Lithophaga* that bore in dead substrates are devoid of shell encrustations, but some dead-substrate species possess coatings fully comparable to those of live-coral borers (pers. obs.).

The boreholes of live-coral *Lithophaga* show distinctive morphological characters. The coral surface immediately surrounding the borehole opening is often depressed into a shallow funnel. This feature is absent in dead-substrate *Lithophaga*. In addition, growth of the coral forces the bivalve to move backwards through the substrate, in order to remain close to the external environment. This, in turn, is required by the relatively inefficient filibranch gills of these bivalves (Carter, 1978). The backwards-boring process causes the bivalve to vacate the anterior region of the borehole. This results in a long anterior extension of the borehole, partly filled with meniscus-shaped calcareous septa and/or loose calcareous deposits (Figure 5H). In Quaternary deposits along the coast of Hilotongan Island, the Philippines, the writer observed weathered sections of large coral boulders containing *Lithophaga* backward-boring tracks reaching approximately 1 m in length. Assuming a rate of backward-boring equal to or higher than that of forward-boring (because of the presence of the siphonal opening, backward-boring necessitates the removal of a smaller volume of substrate per unit of length than forward-boring), the observed length of boring tracks is consistent with observations on the Recent rock-boring species *L. lithophaga* by Kleemann (1973, and references therein), who reported a boring rate in limestone of up to 12.9 mm per year and a life span of up to about 80 years.

Lithophaga lessepsiana is a small Recent species that bores either in living reef corals or in solitary free-living scleractinians of the genus *Heteropsammia* (Arnaud and Thomassin, 1976; Kleemann, 1980). *Heteropsammia*, in turn, is symbiotic with a sipunculid housed in a spirally coiled cavity in the basis of the coral. *L. lessepsiana* bores within the basis of *Heteropsammia*, and grows to a shell length comparable to the coral diameter, probably causing the eventual death of the coral (Arnaud and Thomassin, 1976). When boring in *Heteropsammia*, *L. lessepsiana* lies with the ventral commissure uppermost (Arnaud and Thomassin, 1976). This species is entirely or almost entirely devoid of secondary calcareous deposits of the external shell surface.

The Recent mytilid *Fungiacava* went one step further and evolved into an endoparasite of fungiid corals (Goreau *et al.*, 1976, and references therein). The siphonal opening of this small form communicates with the coelenteron of the host, from which the bivalve draws its food. *Fungiacava* follows the growth of the host by migrating within its borehole to remain near the coelenteron. Like *L. lessepsiana*, it lies with the ventral commissure uppermost. This habit is recognisable in fossils, because of the placement of the siphonal opening of the borehole in a region of the coral skeleton covered by a considerable thickness of soft tissues. In fact, boreholes of *Fungiacava* were described in

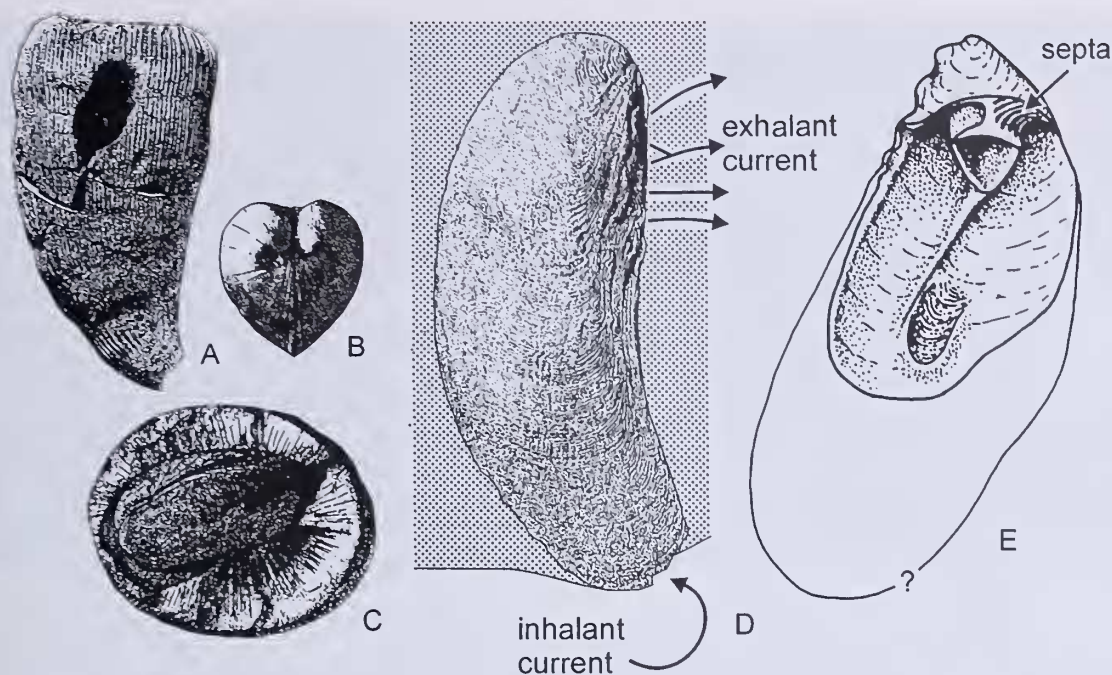


Figure 1. A-C. *Botula hortensis* (Lamarck) symbiotic in *Pattalophyllia* sp., Upper Eocene, Possagno, Italy, (Geologisch-Paläontologisches Institut, Tübingen, Germany, GPIT 1571/2-4). Host coral with siphonal opening of borehole (A), anterior view of shell (B) and shell in place within the borehole (C). Shell length is 19 mm. D. Schematic drawing of *Vulsella vulsella* (Linnaeus) embedded in host sponge, Recent, Cebu Island, the Philippines. The surface of the sponge is at the bottom. Shell length is 4 mm. E. *Stefaniniella colosii* Tavani, Cretaceous, Somalia (modified from Tavani, 1941). Height of the preserved shell portion is 85 mm. The extent of the original shell outline (indicated with a question mark) is reconstructed by analogy with Recent *Vulsella* and other malleids.

Pleistocene fungiids (Goreau *et al.*, 1976).

Botula.—The Eocene mytilid *Botula hortensis* (Figure 1A-C) was a borer obligatorily associated with living solitary corals (Savazzi, 1982b). Unlike other boring bivalves (cf. Savazzi, 1999b, and therein), *B. hortensis* did not secrete a lining onto the walls of the borehole. Instead, the coral host reacted to the presence of the borer by sealing the spaces between adjacent septa with a secondary calcareous secretion in the region surrounding the borehole. This reaction by the host enables one to detect that the coral was alive at the time it was bored. The borehole of *B. hortensis* opens on the side of the coral theca (Figure 1A).

The corals inhabited by *B. hortensis* were soft-bottom forms attached to a substrate only in their juvenile phase and probably capable of active righting. Their theca is horn-shaped, rather than flattened like fungiids. *B. hortensis* had a life orientation with the ventral commissure uppermost (like *Lithophaga* in soft-bottom corals; see above).

Although morphologically similar to other species of *Botula*, *B. hortensis* differs in behaviour and autecology. Recent *Botula* are mechanical borers in soft rocks and packed mud, while *B. hortensis* appears to be a chemical borer, because its shell is thin, has no specialised sculpture, and yet displays no surface wear (Savazzi, 1982b, 1999b).

It is difficult to imagine an evolutionary pathway leading from typical *Botula* to *B. hortensis*. Therefore, it is legitimate to suspect that the morphological similarity of this species with *Botula* is due to convergence rather than

phylogenetic affinity (i.e., that *B. hortensis* is not a true *Botula*), or alternatively, that the life habits of *Botula* in the past were substantially more varied than those of Recent species.

Gastrochaenidae.— This family contains rock and dead-coral borers, as well as several taxa that evolved secondarily into tube dwellers in soft sediments (Carter, 1978, Savazzi, 1982a, 1999b; Morton, 1983). The boring representatives secrete a calcareous lining onto the inner walls of the borehole, and can extend this lining into a chimney-like projection when threatened by the overgrowth of encrusting organisms. The lining is also functional in protecting the bivalve when it becomes partly exposed. This lining became a stepping-stone to the evolution of the tube-dwelling habit, in which the bivalves are encased in a calcareous envelope, or crypt (Savazzi, 1982a).

Freneix and Roman (1979) illustrated Tertiary echinoids containing the calcareous linings of gastrochaenids boreholes, and interpreted this as an instance of parasitism by the bivalves. However, an analysis of this instance shows that the echinoids most likely were dead at the time of boring, and that the bivalves utilised the test as a substrate. In fact, none of these echinoids visibly reacted to boring by the bivalves, which often passed through the test and built calcareous canopies on both its internal and external surfaces. This lack of a reaction is highly unlikely in a living echinoid, since its test is a porous dermaskeleton containing abundant living tissues. Savazzi (1982a, fig. 3E) il-

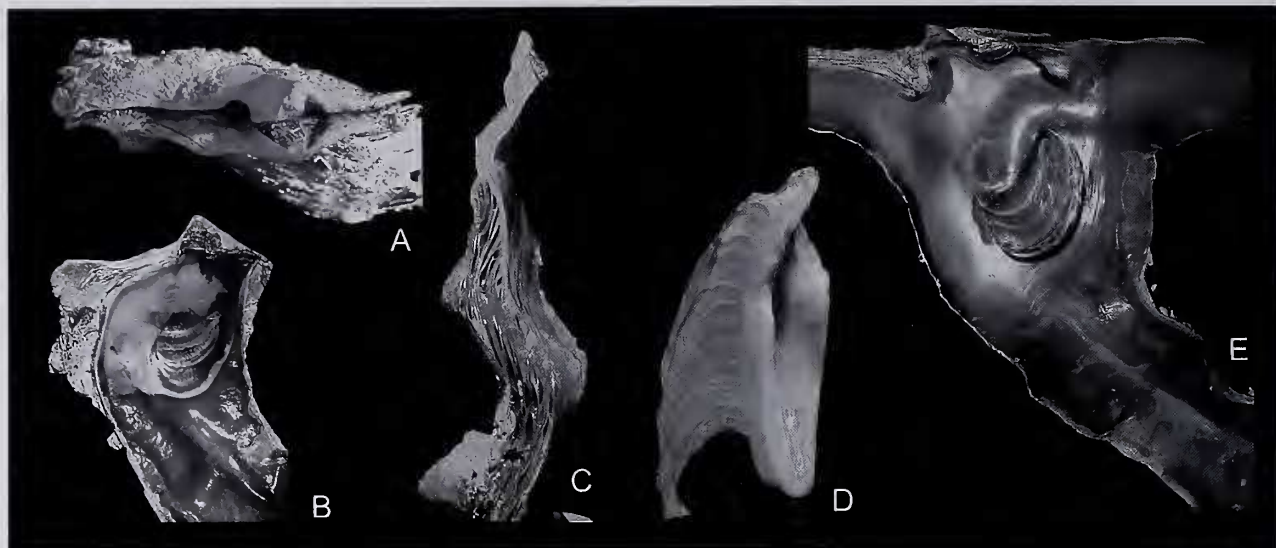


Figure 2. A–B. *Malleus anatinus* (Gmelin), Recent, Cebu Island, the Philippines. Dorsal view with byssal gape (A, $\times 1.2$) and interior of dorsal portion of right valve (B, $\times 0.7$). C, E. *Malleus malleus* (Linnaeus), Recent, Cebu Island, the Philippines, $\times 1$. Interior of right valve of subadult specimen, not yet showing the secondary shrinkage of mantle tissues (see the text for details). D. Unidentified malleid, Middle Eocene, Verona, Italy, $\times 4$.

illustrated a comparable instance of a gastrochaenid boring in the test of a Recent sand dollar (also dead at the time of boring), and building calcareous canopies on both sides of the thin echinoid test (in the illustrated specimen, the test was subsequently destroyed by erosion, leaving an isolated crypt).

Malleidae.—Typical malleids are epibyssate forms. They are characterised by a monovincular resilium, a byssal notch located close to the umbones (Figure 2A), and in several genera by projections of the shell that function as a stabilising surface in connection with an epibyssate or reclining habit (e.g., Figure 2E; Seilacher, 1984). Yonge (1986) described *Malleus* as a semi-infaunal orthothetic form, but the writer's field observations on living *Malleus* in the Philippines confirm Seilacher's interpretation of this genus as an epifaunal recliner. In malleids, the organism often displays a determinate growth pattern, in which the mantle first grows to the full extent of the shell perimeter in order to build the projections along the edge of the shell, and subsequently shrinks to a substantially smaller area of the inner shell surfaces, leaving behind growth lines on the abandoned inner shell surfaces that allow one to detect the stages of this growth process (leftmost region of Figure 2B).

The genus *Vulsella* (Figures 1D, 3F–N) is a malleid endosymbiont in soft sponges (e.g., see Reid and Porteous, 1978, and references therein). The shell is completely embedded in the sponge tissues, and only a short length of the ventral commissure communicates with the external environment (Figures 1D, 3L–M). This genus does not display the shrinking of the mantle tissues in the adult stage displayed by other malleids. The proportions of the shell and its outline are very variable, as a result of irregular growth of the host sponge. Shell height can reach about 100 mm in

the largest specimens, but is usually limited to 30–40 mm.

As verified in living specimens of *V. vulsella* from Cebu Island, the Philippines, the region of exposed commissure is the site of an inhalant water current (Figure 1D). There is, however, no detectable exhalant current along the exposed commissure or the surrounding sponge surface. By letting the bivalve inhale pigment dissolved in sea water, it was found that the sponge tissues facing the posterior commissure of the bivalve (which is deeply embedded within the sponge) absorbed the pigment. Further observation of the sponge in this region showed that it contains numerous openings connecting the postero-dorsal commissure of the bivalve with the canal system of the host. Therefore, *Vulsella* exploits the host sponge as a sink for its exhalant current, and probably takes advantage of the passive flow induced within the sponge canal system by surrounding water currents, in a manner closely similar to that described by Savazzi (1996, 1999a) for the gastropod *Siliquaria*. This flow may reduce the energy expended by the bivalve to strain water. The sponge may gain from the symbiotic association in that the bivalve shells provide a rigid internal framework that allows the sponge to extend in height (Reid and Porteous, 1978). Empty shells of *Vulsella* completely embedded within the sponge are common.

The outer surface of the shell in *Vulsella* bears a sculpture of sharp frills directed obliquely outward (Figure 3N). This sculpture is likely adaptive in greatly increasing the adhesion of the shell to the tissues of the host. It is delicate and always worn away in dead shells found loose on the bottom. Therefore, it is unlikely to be preserved in fossils. The sculpture is prominent in the juvenile stage, and becomes irregular and subdued in the adult stage. This is consistent with the above functional hypothesis, since juveniles are

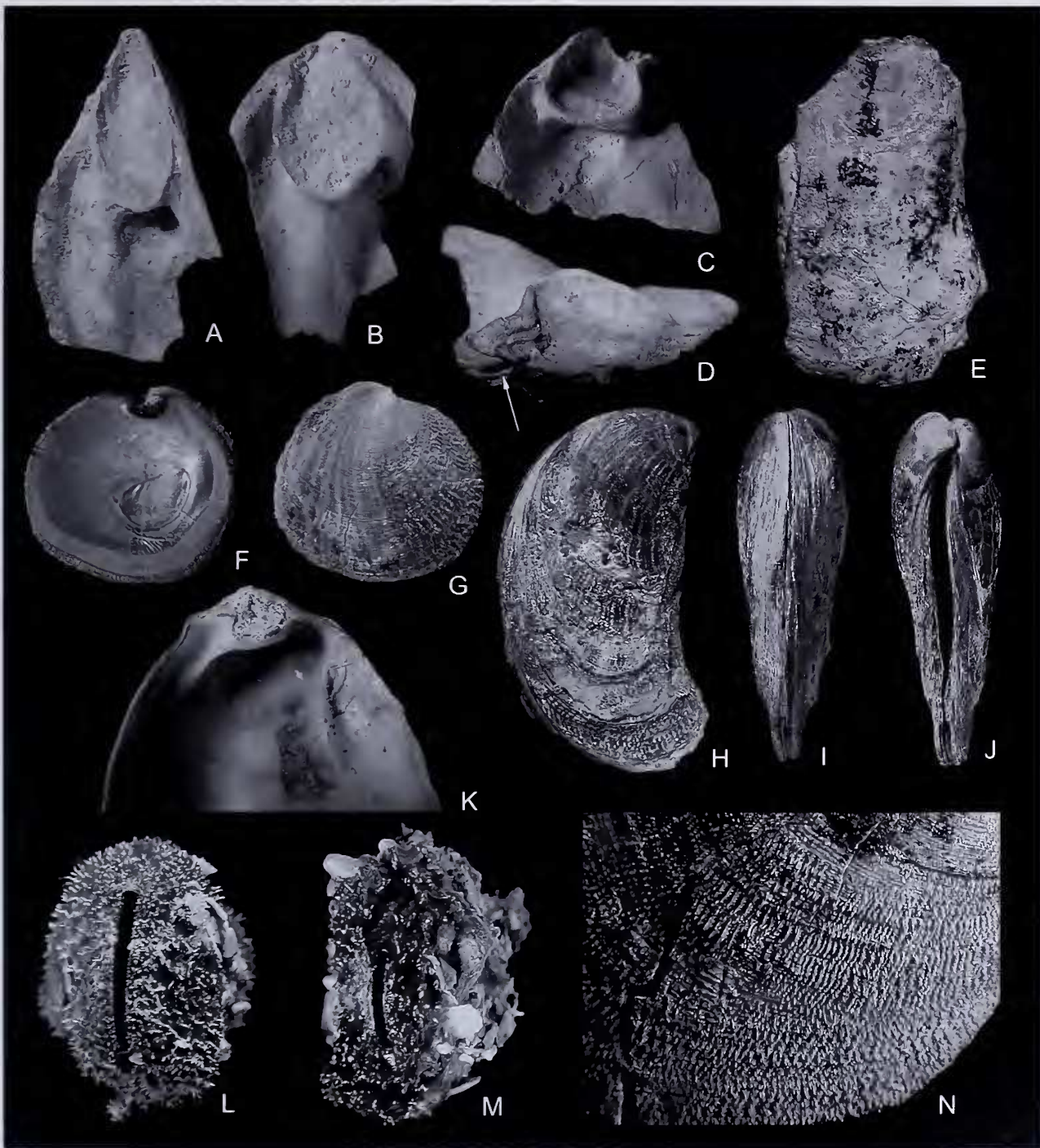


Figure 3. A-E. Unidentified malleid, Middle Eocene, Verona, Italy. Resiliifer and double butress (A-C, $\times 2$; C is viewed from an oblique left-ventral direction), byssal notch (indicated by arrow, D, $\times 3$) and bivalved specimen lacking the hinge region (E, $\times 0.7$). F-N. *Vulsella vulsella* (Linnaeus), Recent, Cebu Island, the Philippines. Interior and exterior of right valve of juvenile (F-G, $\times 2.5$), exterior of adult (H-J, $\times 1.3$), interior of hinge region of right valve (K, $\times 2.5$), ventral commissure of living specimens in host sponge, probably *Ricinia* sp. (L-M, $\times 2$) and detail of sculpture on exterior of juvenile shell (N, $\times 10$).

less deeply embedded within the sponge, and more likely to be broken loose.

The biomechanics and geometry of the shell in *Vulsella* suggest criteria applicable to detect comparable life habits in fossil forms. The resilium of *Vulsella* is unusually large (Figure 3F, K), and grows proportionally larger with age. By comparison, much larger epifaunal forms like *Malleus* have proportionately smaller resilia (Figure 2B, E), in spite of their much thicker and heavier shells. In *Vulsella*, the large resilium is probably related to the fact that the valves must open against the pressure exerted on the shell by the tissues of the host sponge. As a consequence, the resilium in adult *Vulsella* is inserted onto a well developed and thick resilifer, which displaces the ligament ventrally to the hinge line (Figure 3K). The resilifer is almost absent in juveniles (Figure 3F), and the resilium at this stage is inserted close to the hinge line. The shell wall near the resilifer in adults is strengthened against flexing by a buttress deposited onto the inner shell surface (Figure 3K). This buttress, which is absent in juveniles, is located near the anterior side rather than in a medial position.

The buttress, together with the strong resilium and a somewhat thickened dorsal shell region, stiffens this part of the shell. As a result, the ventral commissure closes thanks to the thinner central region of the shell flexing under the contraction of the adductor muscle. This results in closure of the exposed ventral shell gape. A permanent gape remains along the anterior shell margin (which is embedded within the sponge, and stiffened by the nearby buttress). Reid and Porteous (1978) reported the presence also of a posterior gape, but this feature is absent or reduced in the material available to the writer, especially when the valves are adducted and the ventral gape closed. Thus, it appears that the main function of the resilium is to open the valves progressively during growth, in order to allow further shell growth along the ventral margin.

Most fossil malleids were undoubtedly epibyssate or recliners (see Hertlein and Cox, 1969; Seilacher, 1984). A few forms, however, are similar in general shell morphology to *Vulsella*. In particular, the African Cretaceous *Stefaniella* (Figure 1E) is comparable in general shape, but has a zigzag postero-dorsal commissure and a larger size (Tavani, 1941, and references therein; Hertlein and Cox, 1969). The inner shell surface of this genus is characterised by a large resilifer, a roughly medial buttress connecting the resilifer to the shell, and a series of septa spanning the space between resilifer and shell surface in the posterior region (Figure 1E). Tavani (1941) regarded such a chambered structure as absent in the Malleidae, and placed this genus in the separate family Stefaniniellidae, but subsequent authors placed it in the Malleidae.

An imperfectly known, unidentified form from the Middle Eocene of Italy (Figures 2D, 3A-E) is similar to *Stefaniella* in its relatively large size (estimated to about 150 mm in shell height), large resilifer, and septa connecting the resilifer to the shell (Figure 2D). However, its posterior commissure is apparently straight like *Vulsella*, and unlike *Vulsella* and *Stefaniella* it possesses two buttresses (Figure 3A-C). The buttresses have a massive internal structure, and surround the central septate region on either side. Unlike both

Vulsella and *Stefaniella*, this form also displays what appears to be a well developed byssal notch (arrow in Figure 3D). Unlike in epibyssate malleids (cf. Figure 2A), this notch continues in the ventral direction into an extensive permanent anterior gape, which does not agree well with an epibyssate habit in shallow water. It is possible, instead, that this permanent gape was embedded within a sponge, like *Vulsella*. It may be noted that also in *Vulsella* the anterior gape appears to be delimited dorsally by a vestigial byssal gape. A comparable habit is also possible in *Stefaniella*, although it is difficult to decide whether this genus possessed a permanent commissural gape. By analogy with *Vulsella*, the exhalant current in *Stefaniella* would have exited in correspondence with the zigzag portion of commissure. The distinctive zigzag folding of this region of commissure could be an adaptation for increasing stiffness of this shell region.

The Eocene malleid *Euphenax* possesses a lightweight shell with a cavernous outer layer and a chambered inner layer (Hertlein and Cox, 1969). Therefore, a septate or vacuolar structure is not unique to *Stefaniella* and related genera. Such a structure is also found, for instance, in *Malleus* (Figure 2C). The shell of *Malleus* and related forms displays several constructional elements shared by *Vulsella*, *Stefaniella* and the Eocene form discussed above. However, these elements are placed in different positions, and their mechanical effects are therefore different. For instance, the adductor muscle in *Malleus* is located close to the hinge (Figure 2B, E), the vacuolar structure is distributed along the height of the shell with the exception of its dorsal region (Figure 2C), and a buttress-like dorso-ventral ridge stiffens the inner side of the shell, but is located ventrally to the adductor muscle, rather than immediately below the resilium (Figure 2B, E). A true resilifer differentiated from the hinge line is also absent in *Malleus*. All these characters are related to an epifaunal life habit, in which the shell is stiff and opens by flexing the resilium, which does not need to be overly large and therefore allows a placement of the adductor muscle not far from the hinge. Finally, the byssal gape in *Malleus* and related forms is well developed, but clearly delimited from the rest of the commissure (Figure 2A), which shows no other permanent gapes.

Pteriidae.—*Crenatula modiolaris* is a Recent pteriid byssally attached to soft sponges and covered by a thin layer of sponge tissues (Figure 4A-F). The writer observed living *C. modiolaris* in Bantayan Island, the Philippines, and preserved specimens of *C. nakayamai* in museum collections. Unlike *Vulsella*, this species is not deeply embedded, and its shell morphology is therefore relatively unspecialised with respect to epibyssate pteriids. Unlike in epibyssate forms, its shell is often irregular and visibly distorted. Epibyssate forms can be of variable morphology, as a result of different current regimes, but their shell geometry is rarely distorted. This difference is potentially useful in detecting similar habits in fossils. Crevice-dwelling pteriids are also irregular, but in a different manner. For instance, in the latter it is often possible to recognise in the shell morphology irregularities of the substrate to which the shell had to conform. In *Crenatula*, instead, the contours and surfaces are smooth and often characteristically bulging outwards in

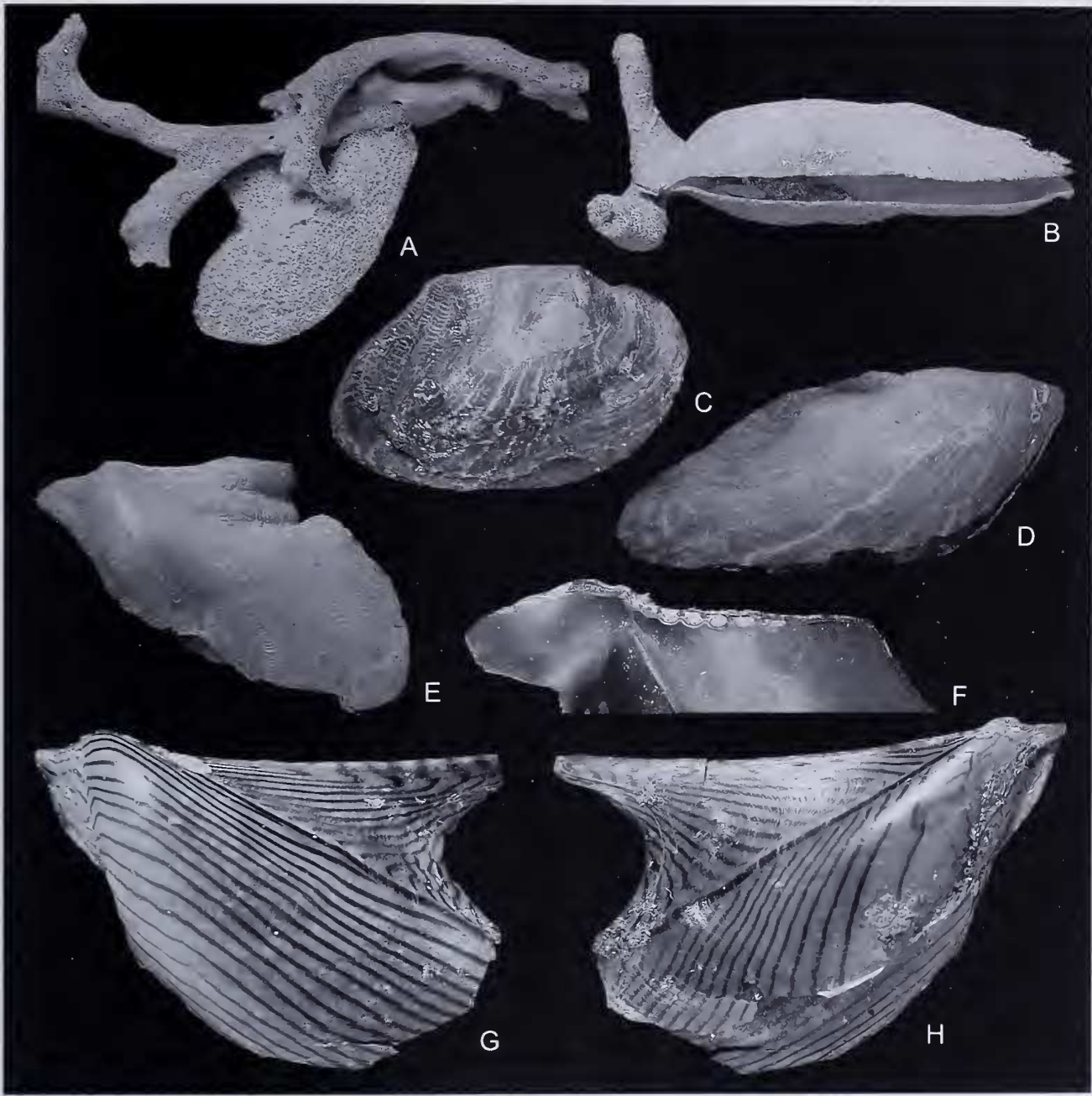


Figure 4. A-F. *Crenatula nakayamai* Kuroda & Habe, Recent, Amami-Oshima Island, Kagoshima Prefecture, Japan (Sakurai collection, National Science Museum, Tokyo, Japan). Dried specimens embedded in host sponge, probably *Haliclona* sp. (A, approximately $\times 1.2$, B, approximately $\times 2$), isolated shells (C-E, approximately $\times 1.6$), and interior of right valve showing the curved hinge line (F, $\times 1.8$). G-H. *Pterelectroma zebra* (Reeve), Recent, Nagai, Kanagawa Prefecture, Japan (Sakurai collection, National Science Museum, Tokyo, Japan). Left (G, $\times 5$) and right (H, $\times 5$) valve of the same specimen.

a balloon-like fashion (see especially Figure 4E). This irregularity may extend to the ligamental area, which may be bent (Figure 4F). In the long run, this situation is incompatible with further growth, because a bent hinge line prevents the valves from opening gradually during growth, in order to

allow the ventral margins to be extended. The thin shell flexes under the contraction of the adductor muscles, and this allows the bivalves to close the ventral commissure even though the hinge line is curved.

The coating of sponge tissues in *Crenatula* may deter

some predators. However, Reid and Porteous (1978) reported that *Octopus* often predate on *C. modiolaris*. There seems to be no possibility for the exhalant current of the bivalve to be led into the canal system of the sponge, since the whole commissure of the bivalve is exposed, except for the hinge and byssal gape. It is possible that the encrusting sponge is effective as visual camouflage against other predators, since the shell colour of *C. modiolaris* always matches that of the associated sponge, which ranges from light brown to almost black (pers. obs. in Bantayan Island, the Philippines). There is no apparent advantage for the host sponge.

Several pteriids are epibyssate on soft corals or other organisms. *Ptereleotroma zebra* possesses an unusual colour pattern (Figure 4G–H) that mimics the hydrozoan substrate. This pattern appears to constitute a visual camouflage (see also Seilacher, 1972, fig. 7G, 10). The fact that this pattern is different on opposite valves (Figure 4G–H) contributes to this function, since an observer sees the pattern on both valves simultaneously through the highly translucent shell. This further hides the shell outline and makes it merge visually against the hydrozoan substrate. Since this specialised colour pattern would not be effective against a different substrate (e.g., rock), it is of potential usefulness as an indicator of symbiotic habits.

Ostreidae.—The Recent *Ostrea permollis* is embedded within soft sponges, in a manner comparable to *Vulsella* (Forbes, 1964, 1966). This bivalve is smaller than *Vulsella* (up to about 25 mm in shell length), and its mantle margins and conchiolin are bright yellow like the surrounding sponge tissues. The shell displays no attachment scar. *O. permollis* grows normally when raised in the laboratory in the absence of a host sponge, and the stomach contents in field-collected specimens consist of phytoplankton (above references). A large sponge may contain hundreds of symbiotic oysters, often stacked parallel to each other in especially crowded areas. The inhalant region of commissure is exposed, while the exhalant current is funnelled into canals of the sponge interior.

The adaptive significance of this association is probably protection from predators for the oyster, and, for the sponge, achieving a stiffening structure without spending energy for its construction (Forbes, 1964, 1966). However, the above authors reported that empty oyster shells, although frequent in the outermost layers of sponge tissues, are absent from its centre. The oyster may additionally profit from passively induced flow within the canal system of the sponge. Therefore, this case can be regarded as convergent with *Vulsella*.

Pectinidae.—The Recent pectinid *Pedum* (Figure 5A–E) is a nestler in living scleractinian corals (Yonge, 1967; Savazzi, 1998). It settles on the surface of the coral, and it becomes gradually embedded by growth of the host (Figure 5A, B). This genus does not abrade the substrate (except to a very limited extent, see Savazzi, 1998), and both valves are almost flat as viewed in section along the dorso-ventral axis. This is a consequence of the lack of substrate abrasion, because growth of a convex, coiled shell requires the umbones to rotate and move away from each other, thus increasing shell inflation in this area (see Savazzi, 1987). *Pedum* dis-

plays also a very limited amount of ontogenetic migration of the shell toward the surface of the substrate (see the space vacated at the bottom of the coral cavity in Figure 5B). These constraints are reflected in a number of peculiar morphological adaptations, such as the anterior auricle of the right valve being located inside the earlier shell cavity and exposed by secondary resorption of the shell wall (Figure 5C). An inequivalve condition is a further consequence of this mode of growth (Figure 5D, E).

The inability to remove any substantial volume of substrate forces the juvenile to gape broadly (Figure 5A), in order to maintain a cavity in the substrate large enough to accommodate the adult hinge region, which, in turn, becomes laterally asymmetric in order to allow the smaller left valve to move ventrally during growth, thus reducing the space needed to allow valve opening. In conclusion, the shell geometry and growth process of this genus are explained by its symbiosis with scleractinian coral and by its inability to abrade the substrate. A more detailed analysis of the biomechanics and growth of *Pedum* was provided by Savazzi (1998).

The Recent *Chlamys acroporicola* (Figure 5F, G) nestles among the branches of living ramose scleractinians like *Acropora*. Its shell is often slightly deformed in the adult, because of space constraints. Such deformations, together with the lack of attachment scars (this species is byssally attached) would be recognisable in fossils. However, in this instance there appears to be no indirect way to infer the association of this species with living coral. This habit may explain how the life habit of *Pedum* evolved (Savazzi, 1998).

Carditidae and other nestlers.—A few other Recent bivalves, like the carditid *Beguina semiorbiculata*, are facultative or obligatory nestlers or borers in scleractinian corals, but their morphology does not seem to be distinctive of these life habits. Several of these forms have been discussed by Savazzi (1999b).

Other embedded bivalves.—Several Recent leptonaceans and galeommataceans live within the digestive tract of echinoderms (especially holothurians) and, less frequently, inside the body of other invertebrates (e.g., Voeltzkow, 1891; Malard, 1903; Anthony, 1916; Bourne, 1906). The shell of these bivalves normally shows no morphological adaptation. *Cycladoconcha*, an endoparasite in holothurians, is an exception. The central portion of its shell bears a large hole as a result of secondary resorption (Spärck, 1931), a character potentially recognisable in fossils.

Ectosymbiotic bivalves

Unionacea.—The glochidium of several Recent freshwater Unionacea is an ectoparasite on fishes. Each valve bears a sharp spear along its ventral margin. The tips of these spears converge toward each other, and allow the valves to grip the host like the tips of tweezers when the adductor muscles are contracted (Kat, 1984). The principal adaptive significance of this adaptation is likely that it provides a means for the molluscs to spread upstream along rivers and streams, which would be problematic for bivalves with a planktonic larval stage and a scarcely mobile adult stage. The fossilisation potential of these larval stages is extremely low, so it is not feasible to ascertain directly when

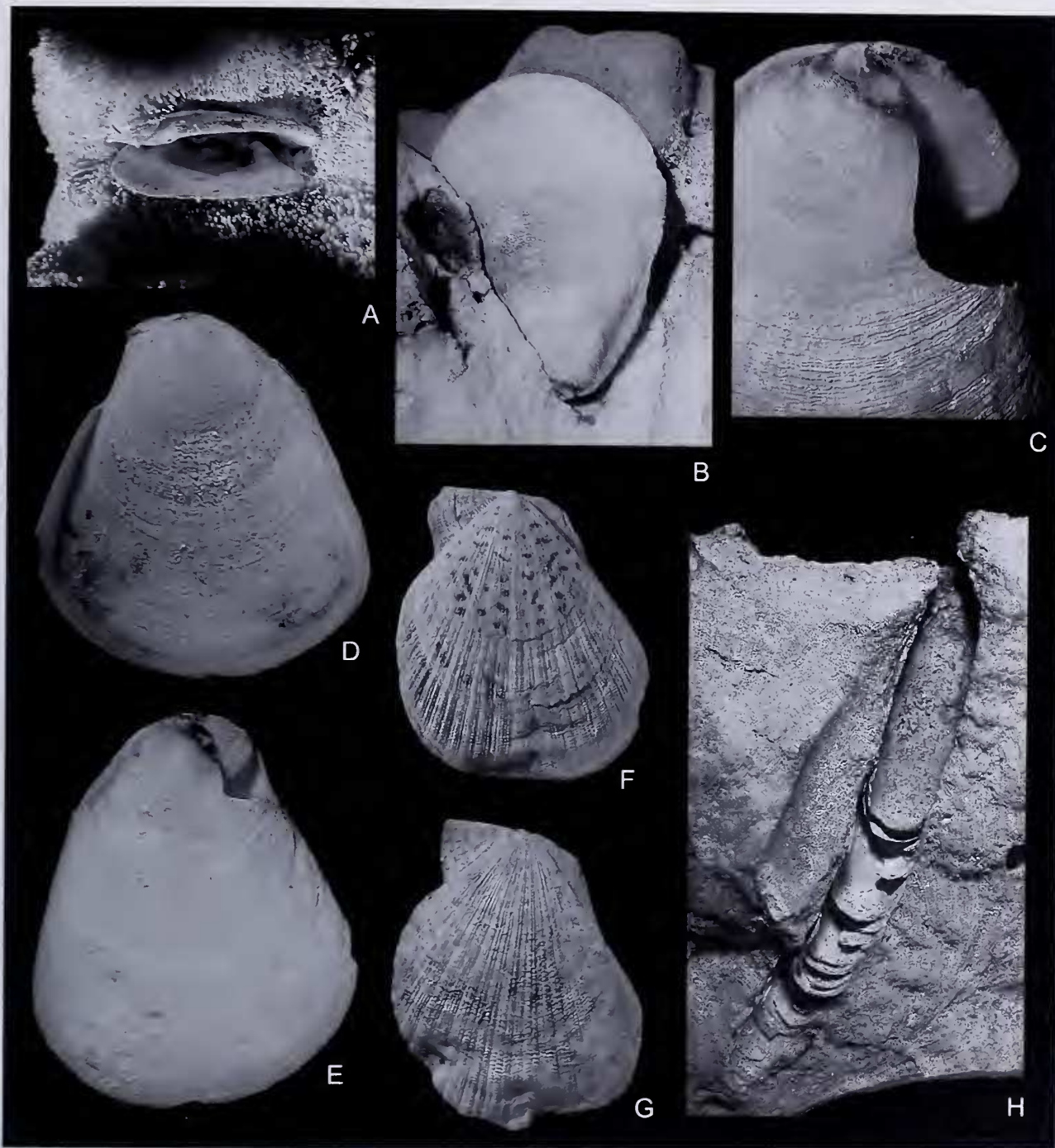


Figure 5. A-E. *Pedum spondyloideum* (Gmelin), Recent, Cebu Island, the Philippines. Juvenile (A, $\times 2$) and adult (B, $\times 1.5$) nestling in coral, detail of auricle of right valve (C, $\times 3$), left and right sides of adult (D-E, $\times 1.4$). F-G. *Chlamys acroporicola* (Iredale), Recent, Cabuyan Island, the Philippines, $\times 2.5$. H. Borehole of *Lithophaga* sp. originally in a living *Porites* coral, subfossil, Cebu Island, the Philippines, $\times 1.3$.

this habit evolved within the superfamily.

Leptonacea and *Galeommatacea*.—These bivalves are typically symbiotic with other organisms. A broad range of hosts has been recorded for Recent representatives. They

include crustaceans (especially brachyurans, macrurans, stomatopods and tanaid shrimps), echinoderms (especially holothurians), sipunculids and polychaetes. Association with other organisms (burrowing sea anemones, phoronids)

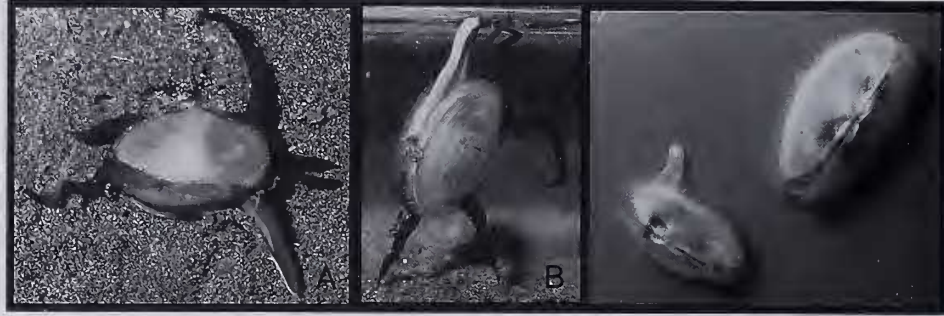


Figure 6. A–B. Living *Scintilla* sp., Cebu Island, the Philippines, $\times 1.4$, crawling on sand (A, with the foot lowermost) and climbing the glass of an aquarium (B, with the white sole of the foot visible). C. Two living specimens of *Galeomma* cf. *polita*, Cebu Island, the Philippines, $\times 3$. The foot is visible in the lowermost specimen. The anterior inhalant (with larger gape) and posterior exhalant mantle regions are also visible. The shells appear “fuzzy” because they are covered by villous mantle tissue.

has been described as well (e.g., see Fischer, 1930; Ohshima, 1930; Popham, 1940; Caullery, 1952; Boss, 1965; Rees, 1967; Morton, 1980, 1988; Noble *et al.*, 1989). Many of these bivalves are associated with a specific type of host, but exceptions are known. *Mysella bidentata*, for instance, has been observed on a large variety of invertebrates, including annelids, sipunculids and echinoderms (Boss, 1965). Leptonacean and galeommatacean bivalves may be byssally attached to the host, or live in its burrow. Several species have been found nestling among epifaunal bivalves or rock and coral crevices, and their hosts, if any, are unknown.

Some leptonaceans and galeommataceans are free-living, and can use the adhesive sole of the foot to creep, and even to climb (Figure 6). Additional peculiarities are constituted by the mantle often covering totally or in part the outer shell surface, and by mantle tentacles, ranging in number from a few to hundreds, which may be functional as a defence against predators (above references). In these superfamilies, the inhalant current enters the mantle in correspondence with the anterior shell slope, and the exhalant leaves from the posterior. The taxonomy of these groups is difficult, and several species are highly polymorphic.

The Recent galeommatacean *Curvemysella paula* (Figure 7A–D) possesses a conspicuously concave ventral margin and a twisted commissure plane. This peculiar morphology is adaptive: this species is byssally attached to the columella of a gastropod shell inhabited by a hermit crab (Morton and Scott, 1989; pers. obs.). The bivalve is located well within the shell, and invisible from the aperture. The commissure conforms to the geometry of the columella and inner shell surface of the gastropod.

Shell morphology in this species is rather constant, but it is not known whether it is genetically preprogrammed or ecotypically determined by space constraints. The somewhat irregular shape of the byssal gape suggests a morphogenetic programme at least partly controlled by the topography of the substrate. The Eocene sportellid *Hindsia*, which possessed a comparably concave ventral margin, may have had a similar life habit. Several other representatives display a concave ventral margin. This fea-

ture may be related to byssal attachment to a convex substrate (e.g., exoskeletal surfaces of arthropods). As discussed by Savazzi (1987), this geometry is adaptive in relieving stress on the byssus, and therefore may enhance the adhesion of the organism to the host.

The galeommatid *Ehippodonta* possesses a shell with a straight hinge line and roughly semicircular and almost flat valves. This genus lives within crustacean burrows, and typically keeps the valves spread apart at an angle of about 180° to each other. The valves cannot be closed and, at maximum adduction, form an angle of roughly 90° to each other. The foot is large, with a wide flat sole used for creeping.

Mysella*, a symbiont on *Lingula

A Recent galeommatid (Figure 7E–I), here identified as *Mysella* sp. because of its hinge structure, was observed by Savazzi (1991) byssally attached to the shells of the living inarticulate brachiopod *Lingula anatina* from the Philippines. This seems to be the only literature record of bivalves symbiotic with brachiopods. The constant placement of these bivalves near the anterior commissure of *Lingula* and their apparently obligatory association with the brachiopod suggest a symbiotic association. Subsequent field work by the writer provided the opportunity for a more detailed investigation, and the results are discussed below.

Material.—In November, 1994, 141 specimens of *L. anatina* were collected manually by digging out sediment from an area of approximately 2 m^2 on a tidal flat in front of the Poor Clare Monastery, Tayud, Cebu Island, Philippines ($10^\circ 21' 15''\text{N}$, $123^\circ 59' 15''\text{E}$). This is the same locality studied by Savazzi (1991). About 20 specimens carrying attached bivalves were placed in aquaria for observation, while the rest were fixed and dried.

Observations on *Lingula*.—Savazzi (1991) reported that *L. anatina* collected in 1990 from the same locality sometimes exceeded 50 mm in shell length. However, in 1994 only 5 specimens in the collected sample exceeded 30 mm, with none reaching 40 mm. A search in the surrounding area failed to produce larger specimens. A subsequent visit in the same locality in 1997 yielded specimens of *L. anatina*

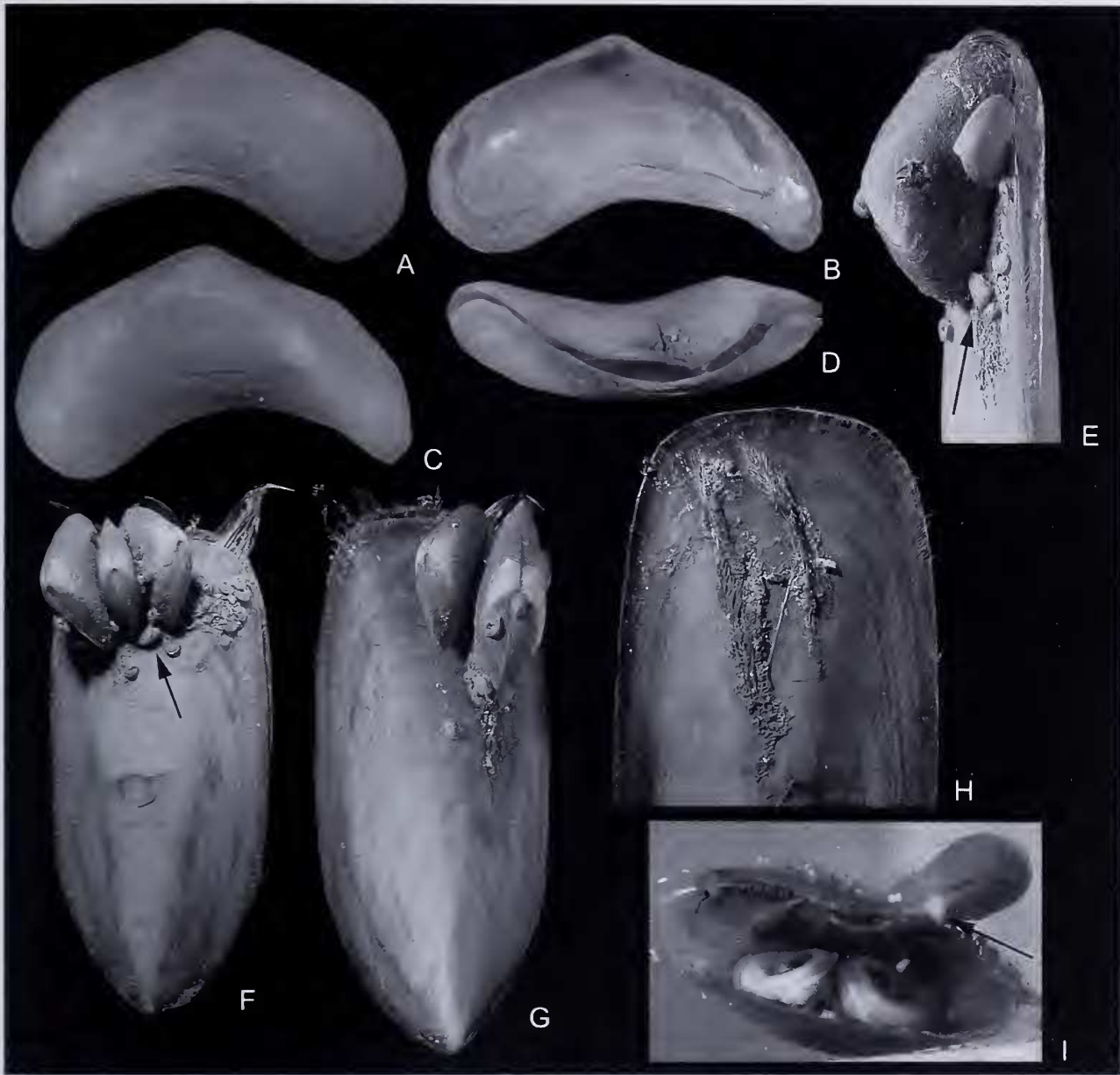


Figure 7. A-D. *Curvemysella paula*, Recent, Cebu Island, $\times 10$. E-I. *Mysella* sp. on *Lingula anatina*, Recent, Cebu Island, the Philippines. Specimens epibyssate on *Lingula* (E, $\times 8$; F-G, $\times 5$, arrows indicate juvenile *Mysella*, small round objects are egg capsules), byssal threads on *Lingula* (H, $\times 8$) and living specimen probing the edge of the *Lingula* mantle with the extended foot (I, $\times 6$, arrow indicates the bivalve foot).

never exceeding 25 mm in shell length. In 1997, *Mysella* sp. was absent from this locality and surrounding areas. The local environment may have become gradually less favourable for *L. anatina* because of the construction of numerous dry piers, which restrict water currents, and an increase in pollution. The gradual decrease in size and abundance of *L. anatina* observed in the test locality may be general in Cebu Island. While this species was available on a daily basis in local fish markets until 1990, it was seldom

seen in 1994 and 1997.

Frequency and distribution of epibionts.—Several *Lingula* collected in 1990 and 1994 carried byssally attached *Mysella* sp. These bivalves were exclusively found attached to living *Lingula*. No other epibionts were observed on *L. anatina* with the exception of two specimens of the gastropod *Calyptrea* sp., but several specimens of *Lingula* carried egg capsules, possibly laid by gastropods (e.g., Figure 7E-G).

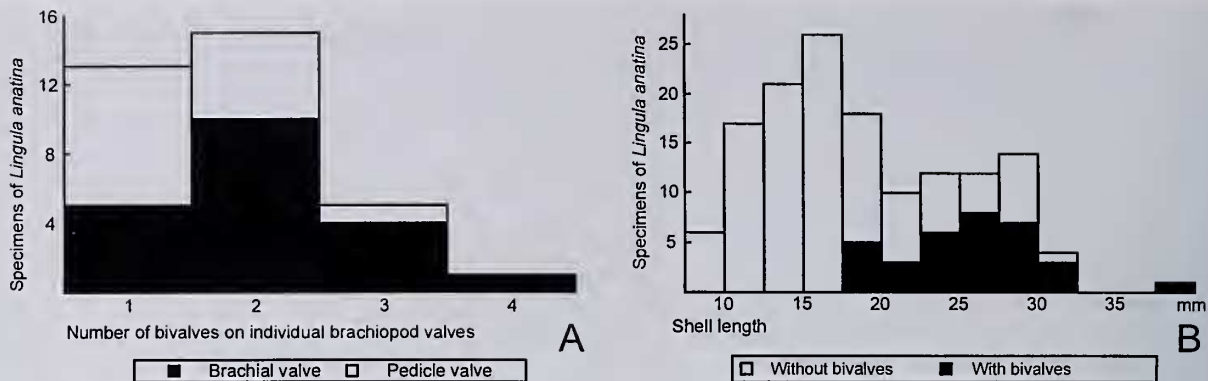


Figure 8. A. Distribution and clustering pattern of *Mysella* sp. on right and left valves of *Lingula anatina*. B. Size distribution of *Lingula anatina* specimens with and without attached *Mysella*.

Mysella sp. is attached indifferently on either valve of the brachiopod (Figure 8A). However, only one specimen of *L. anatina* carried individuals of *Mysella* sp. on both valves. As shown in Figure 8B, the size-distribution of the sample of *L. anatina* is visibly bimodal, with a single outlier at the extreme right of the histogram suggesting a third peak. These peaks likely correspond to year classes. If so, they indicate a rather high yearly mortality (roughly 50% from year 1 to 2, much higher from year 2 to 3). *Mysella* sp. shows a clear preference for larger hosts: 53% of the specimens of *L. anatina* above 20 mm in shell length carry one or more attached *Mysella* sp., while only 5.7% of the specimens below 20 mm do. In total, 23.4% of *L. anatina* carry bivalve commensals. 37 specimens of *Mysella* sp. were collected in total.

Most specimens of *L. anatina* carry one or two bivalves, with a single specimen carrying four (of which one is a small juvenile; Figure 7F). When two or more individuals are present, they usually forms tight clusters. This pattern may result from a preference by *Mysella* sp. to attach near an already present individual, as shown by the different sizes of individuals within the same cluster (Figure 7E–G).

In several cases, the bundle of byssal threads by which *Mysella* sp. is attached to the host continues posteriorly into a trail of old, severed byssal threads (Figure 7G, H). This trail is apparently produced by the migration of *Mysella* sp. toward the anterior commissure of its host. Since *Mysella* sp. is invariably located close to the anterior commissure of *L. anatina* (see also below), this migration must be a response to growth of the brachiopod shell. *Mysella* sp. is preferentially attached in correspondence of the inhalant currents of the host, which enter the shell along the lateral regions of the anterior commissure (see Chuang, 1956; Rudwick, 1970; Savazzi, 1991; and references therein), rather than in correspondence with the centrally located exhalant current.

The shell of *Mysella* sp. is antero-posteriorly elongated, with a straight or slightly concave ventral margin. The umbones are slightly opisthocline and opisthogyrate, and located slightly posterior to the midlength of the shell. The anterior shell slope is slightly more developed than the pos-

terior, which is somewhat truncated. The ventral shell margin is straight or slightly concave, with a thickened shell edge. The periostracum on the outer shell surface is thick and dark brown in colour, and forms a thick carpet of short periostracal shingles arranged in radial lines.

The hinge shows a well developed, elongated anterior tooth and a somewhat shorter posterior tooth on the right valve. The left valve shows corresponding sockets, delimited ventrally by anterior and posterior teeth shorter than in the opposite valve. The ligament consists of a resilium located immediately below the umbones and inserted onto the shell within a depressed ligamental pit. The resilium has a roughly circular median section and is arcuate in antero-posterior view, with the convexity on its ventral side. This suggests that some flexing, in addition to compression, is involved in its function. The ventral side of the ligament bears a central calcified patch, white in colour, on its ventral surface. This is not a true ossiculum or lithodesma, because it does not have well defined edges and cannot be isolated from the rest of the ligament by maceration in alkali (when this was attempted, the calcified patch invariably disintegrated into its constituent aragonitic crystals).

The anterior adductor muscle scar is located in a rather dorsal position, while the posterior is displaced ventrally and close to the posterior shell margin. The area of the anterior adductor scar is substantially larger than that of the posterior. The reduced area of the posterior adductor scar, compared to its anterior counterpart, may be related to the fact that the displacement of the posterior adductor in the ventral direction results in an increase in length of the lever-arm acted upon by this muscle, which in turn lessens its strength requirements. The anterior pedal retractor scar is adjacent to the anterior adductor scar, while the posterior pedal retractor scar is well separated from the corresponding adductor scar, and located more dorsally. This separation is likely a consequence of the unusual placement of the posterior adductor (see above).

The ventral displacement of the posterior adductor muscle (see above) is infrequent in bivalves, and reduces substantially the length of posterior commissure available to the respiratory current(s). However, the posterior commissure in

Mysella houses only the exhalant current, thus reducing the need for an extensive length of commissure to keep the inhalant and exhalant currents separate in the lack of siphons.

When *Lingula* is in life position with the anterior region of the commissure uppermost (see Savazzi, 1991, and references therein), the posterior region of *Mysella* sp. does not face upwards, unlike what was reported by Savazzi (1991). Instead, it is directed downwards. Thus, the life orientation of *Mysella* sp. is essentially the opposite of typical infaunal bivalves.

In the laboratory, *Mysella* sp. is inactive for most of the time. At intervals of several minutes, the anterior commissure of *Mysella* sp. gapes, and the foot is extended toward the anterior commissure of the host. The tip of the foot probes several times in quick succession on the basal region of and between the brachiopod setae (Figure 7I), and is subsequently retracted within the shell. The process lasts 1–2 seconds, may be repeated 2–3 times in succession, and is followed by another period of inactivity. The foot was never extended into the mantle cavity of the host, and the probing activity caused no visible reaction by the brachiopod. On the other hand, artificial stimulation of the setae and mantle of the brachiopod with a flexible bristle in the same region touched by *Mysella* sp. caused an immediate valve-adduction by the brachiopod. The setae, mantle tissues and shell margin of *L. anatina* in proximity of attached *Mysella* sp. showed no visible damage or alteration.

After spending a few hours in aquaria, a few specimens of *Mysella* sp. detached from their host and started to move about epifaunally. Locomotion consists of a forward extension of the foot, adhesion of its tip to a solid object, followed by retraction of the foot, which causes the shell to be dragged forward. The tip of the foot readily adheres to smooth glass surfaces. No burrowing activity was observed, and detached individuals did not reattach to any of the brachiopods placed in the aquaria.

Four preserved specimens of *Mysella* sp. were dissected and their guts examined. They were found to be empty or to contain small amounts of matter, the nature of which was not recognisable under an optical transmission microscope or a dissecting microscope.

Significance of association between *Mysella* and *Lingula*.—*Mysella* sp. likely feeds on mucus and/or on detritus trapped in mucus secreted by *L. anatina*. As described above, the tip of the foot is adhesive, and likely used to collect food particles from the mantle and setae of the host. This feeding activity causes no detectable damage to the host, and might aid in its cleansing. This is apparently the first time the feeding of a galeommatacean on its host was observed.

The preferential placement of *Mysella* sp. near the inhalant currents of *L. anatina* is adaptive in this context. The faeces of *L. anatina* are a potential source of food for a symbiont, but faecal pellets are projected into the water column by quick contractions of the brachiopod valves (above references), and therefore may be difficult or impossible to exploit by an organism attached to the outside of the *Lingula* shell.

The shells of *Mysella* sp. byssally attached on *L. anatina* may hinder or prevent the host from reburrowing when it becomes exposed by sediment erosion. In this situation, it is

possible that *Mysella* sp. detaches itself from exposed *Lingula*, as observed in the laboratory, or becomes dislodged by the energetic burrowing movements employed by *Lingula* (see Savazzi, 1991). It is also likely that *Mysella* sp. hinders the vertical movements of *L. anatina* within its burrow (see also below). A few of the specimens of *L. anatina* showed tufts of byssal threads produced by individuals of *Mysella* sp. that subsequently detached (Figure 7H). The distance of some of these tufts from the anterior commissure of *L. anatina* shows that the brachiopod shell grew substantially after the bivalve detached.

The clustering of *Mysella* sp. provides no obvious advantage in feeding, since adjacent bivalves must then share the same region of host commissure. Rather, it is possible that clustering of *Mysella* sp. makes their individual shells less likely to be dislodged by the movements of *Lingula* within its burrow. This may be especially true of small individuals of *Mysella* nestling close to adult ones (arrows in Figure 7E, F).

The morphology of the burrows of *L. anatina* carrying *Mysella* sp. was observed in three instances. These burrows show a larger diameter and an irregular cross-section in correspondence of the epibionts. These irregularities are potentially preserved in fossilised burrows of linguliform brachiopods (e.g., *Lingulichnites*, see Szmuc *et al.*, 1976). The existence of a comparable association between extinct inarticulate brachiopods and external symbionts, therefore, could be detectable from trace fossils.

Bivalves as hosts to macrosymbionts

The internal surfaces of bivalve shells occasionally display teratological characters produced by worm-shaped organisms living within the mantle or between the mantle and the inner shell surface (Figure 9). These endosymbionts are likely parasites, because the bivalve host is visibly damaged, and likely receives no advantage from the association.

In some Triassic localities of NE Italy, most specimens of megalodontid bivalves display a U-shaped furrow within one valve (or, more rarely, one such furrow in each valve), with the bottom of the U in proximity to the apex (pers. obs.). A comparable type of infestation was described in Pliocene *Isognomon* (Figure 9B, C; Savazzi, 1995). In this case, the parasite body, as outlined by secondary shell secretion of the bivalve, often spanned across the hinge and followed a twisted and snaking pathway along one or both valve interiors. In two specimens, this induced the formation of a teratologic lithodesma, a feature which is absent in normal shells of all representatives of this family, but present in taxonomically unrelated bivalves (above reference).

In a specimen of the Pliocene arcid *Barbatia mytiloides*, tens of parasites were inhabiting the space between mantle and shell (Figure 9A; Savazzi, 1995). It is interesting to note that the parasite did not spread to the myostraca, a situation which probably would have resulted in the death of the host, and that all parasites eventually were sealed off by the bivalve. A morphologically identical reaction to a parasite is observed also in Recent *Scapharca* from Japan (pers. obs.).

It is usually infeasible to decide the nature of these symbionts in fossil material, since their traces on the bivalve

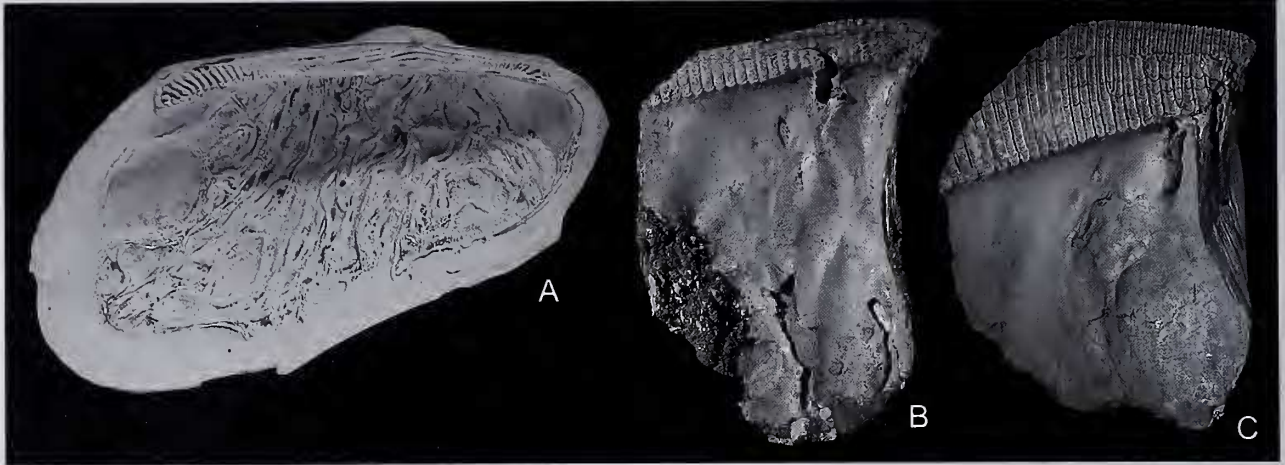


Figure 9. Interior of right valves of bivalves parasitised by worm-like organisms. **A.** *Barbatia mytiloides* (Brocchi), Middle Pliocene, Piacenza, Italy, $\times 1.2$. **B-C.** *Isognomon (Hippochaeta) maxillatus* (Lamarck), Upper Pliocene, Asti, Italy, $\times 0.4$.

shells reveal no morphological features, except the general body shape and size of the symbiont.

Both boring and tube-building polychaetes are frequent on the external surface of bivalve shells, and their distribution provides information on the life orientation and life habits of the hosts. In particular, in semi-infaunal bivalves the presence of polychaetes indicates that the shell region they inhabited was exposed above the surface of the sediment. Usually it is not possible to decide whether these polychaetes are true symbionts (frequently, they may settle on a variety of different substrates and organisms). The preferential settlement of semi-endolithic polychaetes in proximity of the exhalant region of commissure of nonsiphonate bivalves (e.g., Arcidae, pers. obs.), however, suggest that they exploit the faeces and/or pseudofaeces of the bivalve as a food source.

Concluding thoughts

Photosymbiosis has been proposed to explain the large size and/or unusual shell thickness of several fossil bivalves (see above). However, the Tridacnidae are the only Recent bivalves complying with this interpretation. All other documented cases of Recent photosymbiotic bivalves are small forms and, except for *Corculum*, virtually nothing in their shell morphology suggests photosymbiosis.

Stable-isotope analyses could be used to prove photosymbiosis in fossils. This method assumes that the stable-isotope composition of the shells of bivalves housing photosymbionts differs from those of conventional bivalves, since a substantial portion of the carbonate found in the tridacnid shell originates from the photosymbionts. However, with the exception of the Tridacnidae, all Recent photosymbiotic bivalves studied in this respect show isotope profiles similar to those of nonphotosymbiotic forms (above references). In most cases, therefore, proving (or disproving) reliably instances of photosymbiosis in fossil bivalves is

not possible at present, unless photosymbiosis is reflected in morphological adaptations that cannot be explained by other adaptive contexts.

Chemosymbiosis in fossils is even more difficult to prove than photosymbiosis. The only reliable method is probably the study of ichnofossils, especially if associated with specimens preserved in the life position. It may be possible to infer chemosymbiosis in bivalves which, like the Recent *Solemya* and Lucinidae, build specialised feeding burrows with canals that reach deep within the anoxic sediment.

Macrosymbiosis has a better potential than microsymbiosis of being recognised in fossil material, especially if the associated organisms are preserved. It is usually possible to decide, for instance, whether scleractinian coral was dead or alive at the time it was inhabited by a boring or nestling bivalve. Bivalves that bore in living coral display a range of distinctive behavioural and morphological adaptations to this life habit.

It is more difficult to recognise whether a bivalve was embedded in a sponge or other organism with a low likelihood of being preserved. Specialised life habits like the deep embedding of *Vulsella* and *Ostrea permollis* within sponges can be suspected from the lack of a byssal gape or cementation surface, coupled with a shell morphology and size unlikely for a sessile soft-bottom dweller. A few forms taxonomically related and morphologically similar to *Vulsella* may have had comparable habits in spite of the presence of a byssal notch, since byssal attachment on the surface of a sponge in the juvenile stage may have preceded the embedded adult stage, and the byssal notch may have constituted the morphogenetic "trigger" for the subsequent formation of a broader respiratory gape in the same region of the commissure. The presence of unusually strong hinge structures in otherwise thin shells and of adductor muscle scars unusually (for malleids) displaced toward the ventral region corroborate this idea.

Shallow-embedded pteriids within sponges display a

highly variable shell morphology with distinctively bulging irregularities, also potentially recognisable in fossils. Epibyssate attachment to soft-skeleton coelenterates, on the other hand, does not result in comparable morphological characters.

It is usually difficult to decide from shell morphology alone whether an epibyssate pteriid was attached to a living or dead substrate. The cryptic colour pattern of *Pterelectroma zebra*, which provides camouflage against the background of the branched hydrozoan with which the bivalve is associated, seems to be the only exception.

Symbiotic hosts contained within bivalves sometimes can be recognised from teratological reactions of the bivalve. Worms or worm-like organisms living in the mantle cavity, or between the mantle and the shell, often cause recognisable deformation in the shell. Shell-boring or externally cemented polychaetes are usually placed in correspondence to the exhalant current (especially in nonsiphonate bivalves). In addition to allowing one to detect an association between worms and bivalves, these epibionts are useful in helping one to reconstruct the life position of the bivalve with respect to the substrate.

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